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Tiania yunnanense gen. et sp. nov., an osmundalean stem from the Upper Permian of southwestern China previously placed within *Palaeosmunda*

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ABSTRACT

The Permian aged osmundalean fern *Palaeosmunda yunnanense* Tian et Chang has been re-investigated based on the original specimens and demonstrated to represent a new genus within the extinct family Guaireaceae that we name *Tiania yunnanense* gen. et. comb. nov. The stem of *Tiania yunnanense* is small, c. 30 mm in diameter, and comprises an ectophloic siphonostele. Pith is bi-layered and consists of longitudinally elongated cells. Cortex is not differentiated into an inner parenchymatous and outer sclerenchymatous zone characteristic of members of the Osmundaceae, and possesses longitudinally elongated cells and large secretory cells. Leaf traces are numerous (>100) and adaxially curved, with two endarch protoxylem strands upon departing the stele, increasing to more than four protoxylem strands as the trace passes the cortex, all distributed along the adaxial side of the leaf trace. Leaf traces have more-or-less incurved lateral tips, and are encircled by a vascular bundle sheath. A mass of thick-walled, longitudinally elongated cells occur in the adaxial concavity of the leaf trace. Adventitious roots arise singly from the abaxial and lateral margin of individual departing leaf traces, and extend in a sinuous manner horizontally and longitudinally. Abundant tyloses-like contents occur in cells of the cortex and represent the first account of these within fossil Osmundales, but unlike other plant groups in which they occur within xylem, fibre-tracheids and lactifers, in *T. yunnanense* they occur in longitudinally elongated cortex cells where they presumably impeded fungal hyphae growth. Radially aligned 'secondary' parenchyma within the stem appears to represent a wound reaction in the cortex in the living plant. Due to its siphonostele without leaf

gaps, *Tiania* is interpreted as an evolutionary intermediate between the protostelic thamnopterids and the more advanced dictyostelic osmundaleans. Biogeographic implications of *Tiania* are discussed from which it is concluded that the Osmundalean diversity from the Late Permian of South China is unusually high and that these plants are likely to play an increasingly important role in our understanding of the early evolutionary history and systematic relationships of the Osmundales.

Keywords: Osmundales; Guaireaceae; tyloses; wound reaction; Xuanwei Formation; volcaniclastic tuff

1. **Introduction**

Osmundales are an ancient fern lineage that is first recognized in the fossil record during the Lopingian (Late Permian) approximately 260-250 million years ago (mya). Lopingian aged Osmundales are mainly represented by permineralized stems or trunks that have now been identified from the Angaran flora of Russia (see Miller, 1971 for summary), the Gondwana floras in Australia (Gould, 1970) and Brazil (Herbst, 1981), and the southern Cathaysian flora (see Wang et al., 2014). In the Cathaysian flora, permineralized osmundalean stems or trunks have been reported from the Upper Permian of Guizhou and Yunnan provinces in southwestern China. Li (1983) initially described two species preserved in coal balls from the Wangjiazhai Formation and placed them within the genus *Palaeosmunda* as *P. primitiva* Li and *P. plenasioides* Li. Subsequently, Li (1993) reexamined some of the specimens he previously documented

and in doing so erected *Shuichengella primitiva* Li based on specimens of *P. primitiva*. *Palaeosmunda plenasioides* was subsequently re-studied leading to the establishment of the *Zhongmingella plenasioides* Wang et al. (Wang et al., 2014). Thus, both of Li's species of *Palaeosmunda* were subsequently placed within different genera. A third osmundalean species was based on a single specimen preserved in volcaniclastic tuffs from the Xuanwei Formation in southwest China. Unfortunately, this species has been published by Prof. Bao-Lin Tian and his students under three different names; *Palaeosmunda yunnanense* Tian et Chang (in Li and Cui, 1995), *P. xui* Tian et Chang (Tian et al., 1996) and *Palaeosmunda* sp. nov. (Tian and Wang, 1995). The earliest published name of this specimen is *Palaeosmunda yunnanense* Tian et Chang (*in* Li and Cui, 1995) which pre-dates the requirements of Article 43.1 of the International Code of Nomenclature for Algae, Fungi, and Plants (Melbourne Code; McNeill et al. 2012), dealing with "new fossil-taxon published on or after 1 January 1996". Article 43.2. (page 96) states that " a name of a new fossil-genus or lower-ranked fossil-taxon published on or after 1 January 1912 is not validly published unless it is accompanied by an illustration or figure showing the essential characters…". The publication of *Palaeosmunda yunnanense* (1995) comprised a short and accurate description accompanied by five very informative photographic pictures showing general transverse section of the stem, details of the stele and leaf traces, and a longitudinal section of the parenchymatous pith. Therefore, we consider that the name *Palaeosmunda yunnanense* Tian et Chang (in Li and Cui, 1995) is valid.

In this paper we present a re-examination of the original materials of

Palaeosmunda yunnanense Tian et Chang (in Li and Cui, 1995) in order to more accurately characterize the species, and to consider its systematic and evolutionary relationship with other species of extinct and extant osmundalean fern. This study revealed significant differences with the genus *Palaeosmunda* that has led to the attribution of this species to a new genus which we name *Tiania*, resulting in *T. yunnanense* (Tian et Chang) Wang, Hilton, Galtier, He et Shao, gen. et comb. nov.

2. **Materials and Methods**

The specimen described in this paper consists of an osmundalean stem that is permineralized by calcium carbonate and was found in a green to grey and white fine-grained volcaniclastic tuff from the Xuanwei coal mine in eastern Yunnan Province, southwestern China. This locality exposes coals and associated sediments from the Xuanwei Formation that are of Lopingian (Late Permian) age based on biostratigraphy, sequence stratigraphy and regional correlation (Wang et al., 2011). Associated with the stem in the tuff is abundant fine grained plant detritus but these are too fragmentary and poorly preserved to allow detailed identifications to be made.

The specimen was cut by Prof. Bao-Lin Tian in China University of Mining and Technology (Beijing) to reveal transverse and longitudinal sections and then prepared by the acetate peel method (Joy et al., 1956). Exposed surfaces were etched in 5% HCL. The specimen was initially studied by Prof. Tian. The specimen, peels and slides studied by him were deposited in China University of Mining and Technology (Beijing) but some have been lost after Prof. Tian's death (except for five peels that were given

to the first author of this paper by Prof. Tian). These five peels, four are cross sections and one is radial longitudinal section, were mounted on glass slides with Eukitt (O. Kindler GmbH, Freiburg, Germany). The slides were observed and photographed with a Nikon microscope under transmitted light with a Nikon 4500 digital camera. Images were adjusted with Corel Photo-Paint (ver. 12), and plates were constructed with Corel-Draw (ver. 12). Slides used in this study are deposited in the Coal Ball Laboratory of the State Key Laboratory of the Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing under the acquisition numbers WP2L 0029-0032 and WP2-0029.

3. **Systematic Paleobotany**

Order: Osmundales

Family: Guaireaceae Herbst, 1981

Tiania Wang, Hilton, Galtier, He et Shao, gen. nov.

Type species : *Tiania yunnanense* (Tian and Chang) comb. nov.

Generic diagnosis: Stem with an ectophloic siphonostele without leaf gaps. Primary xylem cylinder relatively thin, mesarch and interspersed with parenchyma cells. Pith differentiated into a narrow peripheral zone of smaller thicker-walled cells and a wide central region of larger thin-walled parenchymatous cells. Cortex heterogeneous with dispersed large secretory cells. Departing leaf traces initially C-shaped with more or less incurved lateral tips. Protoxylem strands endarch and located on the concave adaxial surface of the xylem strand of the leaf trace, two in

number upon departing from the stele and increasing to more than four outwards in the cortex. Thick-walled cells filling up the adaxial concavity of leaf trace. Leaf traces numerous, the angle between the leaf trace and the axis in longitudinal section narrow. Single root arising from the cauline stele or abaxial and lateral edge of leaf traces within the innermost part of the cortex and diverging outwards in a sinuous course both in horizontal and longitudinal plane.

Etymology: The generic name is in honour of Prof. Baolin Tian who made available the fossil materials for this study and provided the initial description for this species.

Tiania yunnanense (Tian et Chang) comb. nov. (Fig. 1 and Plates I to V)

Basionym: *Palaeosmunda yunnanense* Tian and Chang, 1995, *in* Li and Cui eds, pages 45-46 and 5 figures (unnumbered).

Holotype: The five slides WP2L-0029, WP2L-0030, WP2L-0031, WP2L-0032 (transverse sections) and WP2-0029 (longitudinal section) = Fig. 1 and Plates I to V in the present paper, and unnumbered figures on pages 45-46 of Tian and Chang *in* Li and Cui, 1995, based on at least two peels taken at a level very close to that in slide WP2L-0031 and WP2-0029 from the present study respectively.

Repository: Coal ball Laboratory Collections, State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing.

Type locality: Xuanwei, eastern Yunnan Province, China

Geological horizon: Xuanwei Formation

Age: Lopingian (Late Permian) (Wang et al., 2011).

Synonyms:

1995 *Palaeosmunda* sp. nov., Tian and Wang, *in* Li, 1995, Plate 60, Figs 1-3

1996 *Palaeosmunda xui* Tian, Wang, Guo, Chen et Zhao, Plate 2, Figs 1-2

Specific diagnosis: Xylem cylinder about 10 tracheids wide in radial direction, consisting of tracheids (up to 80 µm diameter) interspersed with smaller (20-25 µm diameter) parenchymatous cells, sclerenchymatous cells and secretory cells . Narrow peripheral zone of the pith with a radial thickness of 5–8 cells with cell shapes varying from small isodiametrical (25 to 50 µm diameter) to mostly radially elongated (up to 60 µm) inward in transverse section. Thin-walled cells in the central region of the pith usually isodiametric and significantly broader (up to 140 µm diameter). Pith cells typically longitudinally elongated with transverse to oblique end walls; cells of the peripheral zone up to twenty times longer than broad, those of the central zone are broader and shorter, being two to more than ten times longer. Cells of the cortex typically longitudinally elongated. Large secretory cells longitudinally elongated and dispersed in the cortex singly or in groups and arranged in longitudinal files with brown or dark brown contents consisting of tiny particles. Departing leaf traces with parenchymatous and secretory cells internally. Thick-walled cells distributed as a

narrow sheath around the cauline stele and around leaf traces in addition to filling up the adaxial concavity of leaf trace. More than 100 leaf traces in each cross section of the cortex. Xylem strands of the leaf traces encircled by several-layered thin-walled phloem cells. Roots arising from the departing leaf traces.

4. **Description**

4.1. General features

The stem is somewhat elliptical in cross section, about 37×25 mm – 36×28 mm (Fig. 1; Pl. I, 1), and preserved over a length of 45 mm. The elliptical shape is the result of differential compression as shown by the deformation of thin-walled central pith cells abutting thicker-walled cells (double arrows, Plate II, 1), and is considered to be a taphonomic artifact rather than indicative of the stem being elliptical or obliquely sectioned. No mantle of leaf bases or roots is present. However, a few incomplete petiole bases are visible projecting from the stem periphery (PB, Pl. I, 1) and are associated with poorly preserved free roots (arrows, Pl. I, 1). The stele and cortex are complete and well preserved.

4.2. Stele (including pith and phloem)

The stem possesses an ectophloic siphonostele that according to the terminology of Beck et al. 1982 and Schmid 1982 is a ‘stele with a hollow cylinder or tubular mass

of vascular tissue (i.e. with a pith); with only external (outer) phloem, leaf gaps (if present) either overlapping or not, internal endodermis usually lacking'. Like the stem, the siphonostele is elliptical, 7.4 x 5.4 mm in diameter (Fig.1; Pl. I, 2).

4.2.1. Xylem cylinder

The primary xylem cylinder is continuous without leaf gaps, although there are some shallow depressions on the outer surface of xylem cylinder. The xylem cylinder comprises 6–10 (mostly 6–8) tracheids in radial direction and is 0.4–0.6 mm thick (Pl. I, 3; Pl. II, 1; Pl. III, 1-3). In cross section, tracheids vary from nearly round to rectangular or oval, with diameters typically of 25–80 µm (up to 100 µm in a few cases). They are arranged tightly or more or less loosely, with interspersed 'secretory' cells, sclerenchymatous cells and parenchymatous cells (Pl. II, 4; Pl. III, 1-2). The 'secretory' cells with dark contents (Sr, Pl. II, 4; Pl. III, 4) are small, 20–25 µm in diameter, and usually occur in groups. Thick-walled sclerenchymatous cells, with walls up to 10 µm thick (Sc, Pl. II, 4) and thin-walled parenchynatous cells (Pa, Pl. II, 4; Pl.III, 1-2) are isodiametric and small but slightly larger than the secretory cells. In longitudinal section, both secretory cells and parenchymatous cells are longitudinally elongate (Pl. II, 6; Pl. III, 7). The protoxylem elements are located near the outer margin of the xylem cylinder (PX, Pl. II, 1); therefore maturation of the xylem is typically mesarch. Metaxylem tracheid wall thickenings vary from uni- to multi-seriate scalariform on their longitudinal walls (Pl. II, 6, 7; Pl. III, 7). In small tracheids the pits are in uni-seriate vertical alignment and up to bi- to multi-seriate regular or

irregular arrangement in large tracheids. Some large tracheids are also considered as reticulate. Tracheid end walls are typically oblique (Pl. III, 7).

4.2.1. Pith

The pith is elliptical in cross section (Fig. 1; Pl. I, 1-2) with the size of 5.75×4.25 mm , i.e. average 5 mm diameter in cross section. It is divided into two parts, a narrow peripheral zone (P1, Fig. 1; Pl. I, 2) and a broad central region (P2, Fig. 1; Pl. I, 2). The two zones can be distinguished by cell types; cells of the peripheral zone are smaller and have thicker walls (P1, Pl. I, 3; Pl. II, 1), whereas cells of the central region are larger and have thinner walls (P2, Pl. I, 3; Pl. II, 1).

- The peripheral zone is 5–8 cells wide in radial direction (P1, Pl. I, 3; Pl. II, 1), and cells at the outer margin of this zone are usually small and nearly isodiametric, mostly 25×25 – 50×50 µm in cross section , therefore strongly contrasting (long arrows, Pl. II, 1) with the broader innermost tracheids. A characteristic feature is that these cells increase in size and become more or less radially elongated inward (P1, Pl. II, 1), ranging in size from 40×40 – 60×100 µm. These cells are longitudinally elongated, 210-910 µm long and 2.7-22.75 times longer than broad, with horizontal to oblique end walls (Pl. II, 3), and their walls are 3–7 µm thick. The interpretation of this zone of elongated and rather thick-walled cells is problematical. Their longitudinal arrangement suggests that they probably result from the division of procambial cells; they do not show any evidence of pitting and cannot be interpreted as tracheids. Furthermore, they contrast, in size and

arrangement, with the contiguous larger tracheids. These cells may be described as collenchyma-like but this interpretation is questionable.

- Broad central region of the pith: it constitutes more than half of the total diameter of the stele. Its outer part is locally poorly preserved with cells significantly deformed and flattened (D, Pl. I, 3; Pl. II, 1) as a result of vertical compression of the stem. Cells of the central region are usually polygonal in cross section (Pl. II, 1) , typically 30–140 (mostly >100) μm in diameter and have thin walls, usually 2–3 μm thick. Cells of central region of the pith are also typically longitudinally elongated with the length varying from 200–300 μm to more than 1000 μm, and they are often aligned in longitudinal rows (Pl. II, 2). The cells are 2.5–18 times longer than broad and their end walls are horizontal to oblique (Pl. II, 2). The excellent longitudinal section of pith cells originally illustrated by Tian and Chang (1995) strongly supports the interpretation of the central pith cells as parenchymatous. A large cavity, certainly due to tissue decay, occupies the central area of the pith (Ca, Pl. I, 2).

4.2.3. Phloem zone

A continuous zone of light brown coloured cells encloses the xylem cylinder. This zone is narrow and of variable radial thickness, consisting of a few to more than 10 cells. In cross section, the cells of this zone are thin-walled of varying diameter and more or less tangentially elongated (Ph, Pl. II, 5). Although these cells are usually empty, some of them show dark brown contents (arrows, Pl. II, 4, 5). In longitudinal section, cells of this zone are typically longitudinally elongated (Pl. II, 7). Although

sieve cells have not been identified, this continuous zone surrounding the xylem is interpreted to represent the phloem. In addition, the endodermis and/or pericycle may correspond to the outermost layers of this zone but evidence of Casparian bands is not observed.

4.3. Cortex

The cortex is 1.0–1.4 cm thick and is heterogeneous though it lacks a differentiated sclerenchymatous outer and a parenchymatous inner part as seen in members of the Osmundaceae. Cortex consists of parenchymatous cells and thick-walled cells and large secretory cells. Zones of thick-walled cells are distributed around the stele where they constitute the innermost cortex (IMC, Pl. I, 3; Pl. II, 1, 5) and around each leaf trace (Pl. III, 4; Pl. IV, 1-2) as a narrow sheath, and are positioned along the adaxial concavity of the leaf trace (Is, Pl. III, 4; Pl. IV, 1-2). The sheath of thick-walled cells is usually 5-8 cells wide, but around the leaf trace it tapers greatly toward the adaxial side and combines with the thick-walled cells in the adaxial concavity (Pl. III, 4; Pl. IV, 1-2). Thick-walled cells are isodiametric or elliptical in cross section, with diameters of 40–70 µm (Pl. III, 4) and longitudinally elongated with sharp tips and with lengths of more than 1 mm (Pl. III, 5). They are dark coloured and contiguously arranged without intercellular spaces. The thick-walled cells of the adaxial concavity of the leaf traces are usually better preserved than those around leaf traces and the cauline stele (compare: IS, Pl. III, 4; Pl. V, 2 and IMC, Pl. I, 3; Pl. II, 1, 5). The parenchymatous cells are usually elliptical in cross section with their long

axis up to 90 µm and short axis 40 µm or more (Pl. V, 1), and are also longitudinally elongated in longitudinal section where they are 300–400 µm long or more (Pl. V, 3). These cells are brown in colour and more-or-less loosely arranged with intercellular spaces. Dispersed amongst the parenchymatous cells are some large secretory cells that are nearly round or elliptical in cross section, about 100–200 µm in size (arrows, Pl. III, 4; Pl. IV, 2) and longitudinally elongated in longitudinal section where they can be 200–600 µm long (Pl. III, 5). They are often aligned in vertical files (Pl. III, 5) and some are filled with brown or dark densely concentrated tiny particles with diameters of 3–5 µm (Pl. III, 6).

4.4. Leaf traces

The earliest identifiable stage in leaf trace initiation corresponds to a single protoxylem strand in the outer region of the xylem cylinder (Px, Pl. II, 1, 4; arrow, Pl. III, 1). Subsequently, the protoxylem located on the inner side of a narrow band of xylem 2–3 tracheids thick divides into two strands near the extremities of a small parenchymatous area and the narrow xylem band protruds abaxially (Pl. III, 2). One group of cells with dark contents is present on the inner side of the parenchymatous area (Pl. III, 2). This stage corresponds to incipient leaf traces 1 to 4 on Fig. 1 and Pl. I, 2. At a still higher level, there is a lateral opening in the strongly curved outer xylem band (arrow, Pl. I, 3) through which the phloem is connected with the parenchymatous area associated with protoxylem (stage also illustrated at 5, Fig.1 and Pl. I, 2). Finally, there is also an opening on the other side and the narrow curved xylem band separates

as the C-shaped xylem strand of the leaf trace (Pl. III, 3-4). On the general transverse section of the stele (Pl. I, 2), and schematized on Fig. 1, one may recognize the position of incipient leaf traces (numbered 1 to 5) where the outer surface of the siphonostele shows xylem protruberances with internal protoxylem strands, parenchyma and 'secretory' cells.

Leaf traces diverge from the stele at an angle of about 10° (Pl. II, 8) and 103 to 113 leaf traces are visible in the cortex of each stem cross section (Pl. I, 1). One set of 21 parastichies may be counted and this suggests a 13/21 phyllotactic fraction. All leaf traces in the cortex consist of a C-shaped xylem strand that is surrounded by a continuous zone of thin-walled cells interpreted to represent phloem. When leaf traces separate from the stele, they are small, 500–650 μm in tangential dimension, and somewhat elliptical (leaf trace 6 in Fig. 1 and Pl. I, 2; arrow, Pl. III, 3 and Pl. IV, 1; Pl. IV, 4) or nearly half-circular in outline (including xylem strand and surrounding tissue). However as they diverge through the cortex, the leaf traces become shallow C-shaped (Pl. III, 4; Pl. IV, 1) in the inner part to deep C-shaped or horse-shoe shaped (Pl. IV, 2) in the outer part. At this point, leaf traces are much larger, ca. 2 mm wide and the two lateral tips of the xylem strand are more or less involute (Pl. IV, 2). When the leaf trace separates from the stele, the xylem strand is usually 2 tracheids thick in its median region and 2-4 tracheids thick at its lateral edges, with 2 or 3 protoxylem strands (arrow, Pl. IV, 1; Pl. IV, 4). In outgoing leaf traces visible in the median stem cortex (Pl. III, 4; Pl. IV, 1-2), the xylem strand is only 1 (occasionally 2) tracheids

thick and 2 (occasionally 3) tracheids thick at the lateral edges, but it possess 5 or more protoxylem strands located on the adaxial surface of the xylem strand (Pl. III, 4). The phloem enclosing the xylem strand has a radial thickness of 6–7 cells on the abaxial side, with fewer cells on the adaxial side of the leaf traces (Pl. III, 4). When leaf traces separate from the stele, the cells of the phloem on the adaxial side are mostly radially elongated (Pl. IV, 4), whereas those on the abaxial side are tangentially elongated or nearly isodiametric in some cases (Pl. IV, 4). In some instances lacunae are found within the phloem.

A few incomplete petiole bases are visible projecting at the stem periphery (PB, Pl. I, 1). The xylem strand of the petiole base is somewhat V-shaped (LX, Pl. IV, 3).

4.5. Adventitious roots

Adventitious roots originate singly from the lateral abaxial side of leaf traces after they diverge a small distance from the stele (RT, Fig. 1 and Pl. I, 2; Pl. IV, 1). They pass outward through the cortex nearly horizontally and their course is sinuous both in horizontal and vertical plane (RT, Pl. I, 2; Pl. IV, 1). Root traces are oval in cross section and 0.3×0.4 – 0.5×0.7 mm in size (Pl. IV, 5). They are diarch with an oval-shaped protostele consisting of about 10 tracheids (Pl. IV, 5). Larger tracheids of the metaxylem have scalariform to reticulate pitting. Around the protostele is a zone of isodiametric and thin-walled cells. The zone is relatively variable in radial thickness, ranging from 3-5 cells. These cells probably represents the phloem and the inner cortex though no definite endodermis between of them. The outer cortex is about 50–130 μm

thick and consists of small fiber cells. There is no evidence of a root mantle however some free roots (arrows, Pl. I, 1) are visible but these are poorly preserved (Pl. IV, 3).

4.6. Tyloses-like contents

Most of cells in the cortex, including the parenchymatous cells and thick-walled cells that form the sheath surrounding the cauline stele and the leaf traces, as well as thick-walled cells in the adaxial cavity of the leaf trace, are filled with tyloses-like contents. These tyloses-like contents are usually polygonal and isodiametric in shape, with a diameter of 20–30 μm, in both cross section and longitudinal section. There are 4–10 of these structures in each cellular lumen in cross section (Pl. V, 1, 2). However in longitudinal sections of cells these structures are more numerous (Pl. V, 3). These tyloses-like contents are distributed widely and they can be found in cells with different size and in various places. The outline of cortical cells is sometimes obscured for the existence of these tyloses-like contents (Pl. V, 1, 3).

4.7. Radially aligned parenchyma

Some areas of parenchyma with radially aligned cells are present in the cortex of the present specimen. They usually occur at the position of one leaf trace in the outer part and sometimes also on the edge of the cortex (SP, Pl. I, 1). Cells are usually aligned in radiating rows and typically without tyloses-like contents. The vascular bundle of the leaf trace is sometimes completely obliterated by this proliferating tissue (SP, Pl. V, 4). In transverse section these areas are 3–5 mm broad.

5. DISCUSSION

5.1. Taxonomy

This fern was initially attributed to the genus *Palaeosmunda* Gould (1970), however our re-investigation of the specimen justifies the attribution to the new genus *Tiania* characterized by a strictly ectophloic siphonostele without leaf gaps. It differs from *Palaeosmunda* which possess an "ectophloic, generally dictyostelic, siphonostele, a xylem ring consisting of 14-28 more or less contiguous radial strands and 0-13 leaf gaps" (Gould 1970). The comparison of our Fig.1 (*Tiania*) with Fig. 2A (*Palaeosmunda*) clearly illustrates the difference in stelar organization between the two taxa. Moreover, in *Palaeosmunda* the cortex is differentiated into inner parenchymatous zone and outer sclerotic fibrous layer, the petiole bases are stipulate, and the stem is surrounded by a mantle of leaves, all features which do not exist in *Tiania.* We consider that all these differences support the generic distinction of this taxon.

The stem of *Tiania* possesses an ectophloic siphonostele and many adaxially curved leaf traces with protoxylem strands distributed along their adaxial side as is typical of stems of the Osmundales *sensu* Miller (1971) and the Guaireaceae and Osmundaceae (Herbst, 1981; Tidwell and Ash, 1994). Stems of these families differ in the organisation and structure of the cortex and of the petiole bases. Members of the Guaireaceae have a cortex that is undifferentiated or weakly differentiated into an inner and outer zone, and lack stipular wings and sclerotic rings that surround the vascular

bundle of petiole bases (Tidwell, 1991; Tidwell and Ash, 1994). In contrast, the cortex is conspicuously differentiated into an inner parenchymatous zone and an outer sclerenchymatous zone with well developed stipular wings and sclerotic rings in the petiole bases in the Osmundaceae (Tidwell and Ash, 1994). The cortex of *Tiania yunnanense* is not differentiated into inner parenchymatous or outer sclerenchymatous zones. Where known the sclerotic ring surrounding the vascular bundle in the petiole base in the Osmundaceae is derived from the outer sclerenchymatous cortex of the stem. Since our material lacks a differentiated outer sclerenchymatous zone, it is likely that the divergence of the leaf trace and its accompanying tissues is unlike the Osmundaceae. This supposition is confirmed by a few incompletely preserved petiole bases located at the edge of the present stem in which no sclerotic rings have been observed. The available evidence suggests that *Tiania yunnanense* belongs to the Guaireaceae rather than to the Osmundaceae.

To date six genera have been assigned to the Guaireaceae, namely *Guairea* Herbst, *Lunea* Tidwell, *Donwelliacaulis* Ash, *Itopsidema* Daugherty, *Shuichengella* and *Zhongmingella* (Tidwell and Ash, 1994; Wang et al., 2014). There are several unique features that distinguish our specimen from each of the above mentioned genera, namely 1) the presence of a bi-zoned pith consisting of longitudinally elongated parenchymatous and probable collenchymatous cells, 2) thick-walled and longitudinally elongated cells in the adaxial concavity of the leaf trace, and 3) longitudinally elongated cells and large secretory cells in the cortex. The stelar type is also an important character used to distinguish genera within the Guaireaceae. The

present specimen possesses an ectophloic siphonostele without leaf gaps in the primary xylem cylinder, unlike *Guairea* and *Lunea* that have an ectophloic dictyoxylic siphonostele with distinct leaf gaps (Herbst, 1981; Tidwell, 1991), and *Zhongmingella* that has a dictyostele with distinct leaf gaps (Wang et al., 2014). *Donwelliacaulis* possesses a much thicker primary xylem cylinder, up to 4–5 mm (Ash, 1994) than the present specimen whose primary xylem cylinder is only 6–8 tracheids or 0.4–0.6 mm thick. Furthermore, the primary xylem cylinder of *Donwelliacaulis* is exarch, a unique feature in stems of Osmundales whose primary xylem cylinder are typically mesarch (Miller, 1971). *Shuichengella* has a mixed pith consisting of tracheids, parenchymatous and sclerenchymatous cells (Li, 1993), which is very different from the bizoned parenchymatous pith of *Tiania yunnanense*. *Itopsidema* is comparable to the present specimen in several aspects: in both the primary xylem cylinder is thin (1 mm thick in the former and 0.4-0.6 mm thick in the latter), both lack leaf gaps and have longitudinally elongated cells in the pith and the vascular bundle in the petiole is surrounded by a sheath of sclerotic cells (Daugherty, 1960). At last, more than one hundred leaf traces are present in the stem cortex in both cases. However, detail of leaf trace emission, described as “oblong” in the inner cortex, is not well documented in *Itopsidema* which was regarded as a possibly non-osmundaceous fern by Miller (1971). Furthermore, in *Itopsidema*, the pith contains rare reticulate tracheids, there are abundant schizogenous mucilage ducts in the ground tissue of petioles bases, gland-tipped multicelled spines occur on the stem and petiole bases, and the vascular bundle in the petiole base is mushroom-shaped with the lateral tips conspicuously

outcurved (Daugherty, 1960). All these features are unknown in *Tiania*.

In all members of Guaireaceae the cortex consists of isodiametric or slightly longitudinally elongated parenchymatous cells except *Tiania* in which cells of the cortex are conspicuously longitudinally elongated. In some trunks or stems of basal members of the Osmundales, the cortex consists of longitudinally elongated sclerenchymatous cells or thick-walled cells (Wang et al., 2014). For instance, the middle cortex of *Rastropteris* (Galtier et al., 2001) from the Cisuralian (Early Permian) of North China, a trunk similar to *Grammatopteris* Renault, consists of relatively thick-walled and longitudinally elongated collenchyma-like cells. It is possible that the cortex consisting of longitudinally elongated cells in the present specimen represents a feature that is derived from an ancestor with a cortex consisting of longitudinally thick-walled cells, whilst other members of the Guaireaceae with the cortex consisting of isodiametric cells could have evolved from a taxon similar to the present specimen.

Considering the differences listed above, it is not possible to attribute the present specimen to any known genus of Guaireaceae. As a result, we propose to erect the new genus *Tiania* Wang et al. and the new combination *Tiania yunnanense* (Tian et Chang) gen. et comb. nov. to accommodate this specimen.

5.2. Evolutionary significance

Tiania has an ectophloic siphonostele without leaf gaps which represents a rather unique structure within osmundalean ferns where the absence of leaf gaps is generally associated with protostelic stems. It is of interest to compare *Tiania* to thamnopterid

ferns traditionally used (e.g. Bierhorst, 1971; Gould, 1970; Miller, 1971) to illustrate primitive evolutionary stages, in stele and leaf trace. *Thamnopteris schlechtendalii* (Fig. 2B) and *Zalesskya diploxylon* (Fig. 2D) are protostelic with an outer cylinder of long tracheids surrounding a central column of short elements, 2 to 5 times as long as broad; in both cases the central 'tracheids' have a diameter larger than the outer tracheids. We agree with Miller (1971) and consider this central xylem as evidence of evolutionary change toward pith tissue. This is quite different from the situation in *Tiania* (Fig. 1) devoid of central short pitted cells. In *Zalesskya gracilis* (Fig. 2C) the difference between the two zones is not well marked and the large diameter central tracheids, 10 to more times longer than broad, are more similar to outer tracheids. Furthermore, in this species there is a large central cavity, exceeding half of the xylem ring diameter; a very narrow zone of distorted cells (X, Fig. 2C) lines the innermost tracheids. It is unfortunate that this specimen of *Z. gracilis* was not studied in detail because there is no evidence that they are really "crushed tracheids"; they may represent the remains of a decayed wide central pith; this would imply that *Z. gracilis* was not protostelic but siphonostelic and therefore more comparable to *Tiania*. Furthermore, in *Thamnopteris kidstonii* Zalessky (1924) parenchyma occurs within the inner xylem, and this was emphasized by Gould (1970) as one stage in the development of the ectophloic dictyoxylic siphonostele.

Finally, it is tempting to interpret *Tiania*, with its central parenchymatous stelar tissues, as a new evolutionary intermediate form between the protostelic thamnopterids and the more derived ectophloic dictyoxylic siphonostelic forms like

Palaeosmunda. The absence of anypitted elements within the pith of *Tiania* suggests that in this fern the central cells, derived from procambial cells, did not differentiate in to tracheids. The pith of *Tiania* consists of longitudinally elongated cells, most of which are arranged in vertical files. It must be noted that such an arrangement occurs in the extant species *Osmunda javanica* (Hewitson, 1962), although the pith cells are not differentiated into a thicker-walled peripheral zone and a thinner-walled central part.*Tiania* is also evolutionary significant with regard to leaf trace emission. The primitive condition is shown by thamnopterids with the departing solid oval leaf trace containing one central mesarch protoxylem (Fig. 2 B) which becomes endarch (Fig. 2 C-D) and bifurcates as the leaf trace passes through inner cortex. In contrast, the departing leaf traces of *Tiania* are initially C-shaped with two endarch protoxylem strands and this represents a very advanced condition within Osmundales.

Finally, considering the features discussed above, *Tiania* represents a new evolutionary level above thamnopterids but below *Palaeosmunda* and osmundaleans which possess the characteristic osmundaceous dictyostelic anatomy.

5.3. Distinguishing genera from South China from other phytogeographic realms

Including *Tiania*, seven genera have now been circumscribed within the Guaireaceae, among them three from the Upper Permian of South China and four from Upper Paleozoic to Mesozoic of Tasmania and North and South America. The genera from China are different in several aspects. Stems of the Chinese genera (*Shuichengella*, *Zhongmingella* and *Tiania*) are small with the diameters up to approximately 4 cm; leaf traces have enrolled lateral tips; there are a small number of

root traces in the cortex of the stem and no mantle of petioles and/or roots have been found. In contrast, genera from North and South America and Tasmania have stems that are somewhat larger, with diameters up to 22 cm in *Donwelliacaulis chlouberii* Ash, up to 10 cm in *Itopsidema vancleavei* Daugherty, 9×6.5 cm in *Guairea millerii* Herbst and 9 cm in *G. carnieri* (Schuster) Herbst, while *Lunea* Tidwell from Tasmania is smaller and only 1.2–4.5 cm in diameter; the lateral tips of the leaf traces and especially of the petiole bundles are more or less outcurved; there are abundant root traces in the cortex of the stem and there is a distinct mantle of petioles and/or roots around the stem. Tidwell (1991) emphasized the outcurved lateral tips of the leaf traces and petiole bundles in genera *Guairea*, *Lunea*, *Donwelliacaulis* and *Itopsidema* and suggested that it may represent a diagnostic character for the Guaireaceae. Our observations indicate that there may be two distinct groups within the Guaireaceae, one represented by genera from China that are mostly small-sized with distinct enrolled leaf trace lateral tips, fewer root traces in the cortex and probably lack a mantle of leaf traces and/or roots. The second group comprising the Tasmania and North and South American genera that are mostly large-sized with more or less outcurved lateral tip of leaf trace and petiole bundle, and with abundant root traces in the cortex and a mantel of leaf traces and/or roots.

5.4. "Secondary parenchyma" in the stem cortex

Areas of tissue with radially aligned cells in the cortex have not been previously reported for fossil osmundalean trunks or stems. However, it is not unusual for these

types of cells to occur in the Psaroniaceae. Morgan (1959) reported secondary parenchyma in *Psaronius blicklei* Morgan from the Pennsylvanian of North America that develops in the ground tissue or around the meristeles. The function of this tissue is not clear and Morgan (1959) suggested that some of the secondary parenchyma might be a reaction to wounding. In *Tiania*, the secondary parenchyma is mainly developed around leaf traces in the outer part of cortex where the levels of preservation are, on the whole, not as good as that of the inner part of the cortex. It seems to support Morgan's (1959) opinion that the secondary parenchyma in the present specimen might be a reaction to wounding, possibly through herbivory, or external decay while the plant was alive.

5.5. Tyloses-like contents

Tyloses are cellular constructions or cell ingrowths of living wood parenchyma into the cavities of xylem conducting cells . Tyloses are mainly reported in angiosperms, but they also occur in other plant groups from the Paleozoic including lignophytes such as *Protopitys* Goeppert (Scheckler and Galtier, 2003) and the filicalean fern *Ankyropteris* Stenzel (Phillips and Galtier, 2011). The contents in some cortical cells in *Tiania* resemble tyloses in their size, structure and organization. If correctly interpreted as tyloses, their occurrence in cortical cells would contrast from tyloses reported in the vessels or tracheids, mainly of the secondary xylem and in some cases the primary xylem, of angiosperms, lignophyte and ferns as mentioned above. There seems to be no reports of tyloses from cortical cells although tyloses have been

interpreted in non-xylem conducting cells such as fibre-tracheids and laticifers (Gottwald, 1972; Carlquist, 1996). Xylem conducting cells, fibre-tracheids and laticifers are all longitudinally elongated cells as are the cortical cells of *Tiania*, so our interpretation of these as tyloses is consistent with their position within similarly structured cells.

In living plants tyloses can impede fungal hyphae growth in damaged or traumatized wood (Canny, 1997; Jaquish and Evers, 2001), and it is likely that the tyloses-like contents in the cortical cells of *Tiania* had the same function. Fungal hyphae are rarely seen in *Tiania* making this assumption plausible.

5.6. The growth habit of Tiania xuanweiensis

The present specimen is nearly complete and fairly well preserved, however it remains uncertain if there was a mantle of leaf traces and/or roots when the plant was alive, which was subsequently lost, or if the plant did not possess a mantle, as suggested by Li (1983, 1993) for *Shuichengella* and *Zhongmingella*.

In *Tiania*, root trace divergence from the inner to the outer part of the stem is nearly horizontal and according to Miller (1971) this indicates a rhizomatous habit. However, in this plant the leaf trace and petiole base arrangement are very regular suggesting that the small stem was certainly erect.

The root trace divergence through the cortex in the present specimen is different from many other rhizomatous ferns in that in a sinuous course both in vertical and horizontal planes, so it is rare to see a continuous root trace either in a transverse or

in a radial section of the stem. By contrast, in *Zhongmingella* (Wang et al., 2014: Figure 2A) and *Grammatopteris rigollotii* (Galtier et al., 2001: Figure 21), root traces mostly extend outward in the cortex in a straight or slightly wavy course. If this sinuous course of root traces in *Tiania* reflects the plants growth habit or environment in which it lived remains uncertain.

5.7. Osmundalean diversity based on the anatomically preserved plant fossils within the Cathaysian Flora

Possible osmundalean impression/compressions have been recorded through Permian Cathaysian Flora and they are mostly vegetative fronds, i.e. *Cladophlebis* Brongniart, including at least 13 species that distributed from the Shanxi Formation or equivalent strata (Kungurian-Roadian stages of Early-Middle Permian) to the upper part of Xuanwei Formation or equivalent strata (Wuchiapingian-Changhsinghian stages of Late Permian) (Sun et al., 2010). Only one species of possible osmundalean impression/compression fertile frond, *Zhongzhoupteris caudatus* Yang, was reported from Shenhou Formation (equivalent to Shanxi Formation) in Yuzhou, Henan Province, North China. However no in situ spores were gained from the species, its relationship with Osmundales remains uncertain (Yang et al., 2006). Agreeing with Miller (1971), we caution against assignment to Osmundaceae of foliage unless it is nearly identical to that of a recent species or is associated with or in connection with other organs of definite affinity within the group.

Anatomically preserved osmundalean fossils within the Cathaysian Flora are

mainly permineralized trunks or stems. Three genera of osmundalean ferns are now known from the Late Paleozoic Cathaysian flora of southern China and are assigned to the Guaireaceae, namely *Tiania*, *Shuichengella* and *Zhongmingella*. These occur in the Lopingian sedimentary succession of eastern Yunnan and western Guizhou provinces in southwestern China. However, the remaining members of the Guaireaceae (*Guairea*, *Donwelliacaulis*, *Itopsidema* and *Lunea*) are discontinuously distributed geographically across a much larger area that includes the Americas and Tasmania, and stratigraphically from the Lopingian to the middle Jurassic. Amongst the non-Chinese members of the Guaireaceae, only *Guairea* is from the Upper Permian, while the remaining taxa (*Donwelliacaulis*, *Itopsidema* and *Lunea*) range from the Triassic to middle Jurassic. In addition to the three species reported from China, i.e. *Shuichengella primitiva* (Li, 1993), *Zhongmingella plenasioides* (Wang et al., 2014) and *Tiania yunnanense* (this paper), additional specimens within our collections suggest that several new taxa of Guaireaceae also exist in this area as well. Therefore, the diversity of permineralized osmundalean ferns from the Lopingian of eastern Yunnan and western Guizhou provinces may represent a significant radiation event with implications on the origin and early evolution of the Guaireaceae. This contrasts the Ural region of Russia where up to 7 genera and 11 species have been described, but these belong to the Osmundaceae, not the Guaireaceae. It is quite possible that Ural region is the most important area for determining the origin and early evolution of the Osmundaceae. As additional material becomes available it will become clearer if the Lopingian of eastern Yunnan and western Guizhou provinces of China have the most

important strata for providing information on the origin and early evolution of the Guaireaceae.

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Figure captions:

Fig. 1. Camera lucida drawing of the stem of *Tiania yunnanense* gen. et comb. nov. showing gross organization of the ectophloic siphonostele and innermost part of cortex corresponding to Plate I**,** 2. Numbers 1 to 7 indicate successive incipient and departing leaf traces. Dotted line separates peripheral zone (P1) and central region (P2) of the pith. Px=protoxylem, RT=Root trace, Sr=secretory cells, XC=xylem cylinder. Scale bar = 1mm.

Fig. 2. Comparison, at the same magnification, of partial transverse section of stelar tissues and departing leaf traces in members of the Guairiaceae. A, *Palaeosmunda playfordii* (redrawn from Gould 1970, text-fig. 4A); B, *Thamnopteris schlechtendalii* (drawn from Kidston and Gwynne-Vaughan 1909, Plate I); C, *Zalesskya gracilis* (drawn from Kidston and Gwynne-Vaughan 1908, Plate I); D. *Zalesskya diploxylon* (drawn from Kidston and Gwynne-Vaughan 1908, Plate IV). OX= outer xylem; CX=central xylem of short pitted cells; IX=inner xylem; X=supposed "crushed tracheids" on Fig. C only. Scale bar = 1 mm.

Plate I. Stem of *Tiania yunnanense* gen. et comb. nov. .

1. Cross section showing siphonostele (ST) with pith (P), homogeneous cortex with root traces (RT) and numerous leaf traces (LT); at the periphery, a few petiole bases (PB), areas of radially aligned parenchyma (SP) and free roots (arrows). Slide WP2L-0029, scale bar = 5 mm.

2. Enlargement of the central part of Plate I, 1, corresponding to the camera-lucida drawing of Fig. 1, with corresponding numbering of leaf traces (1-7); Ca= large air cavity in the centre of the pith. Slide WP2L-0029, scale bar = 2 mm.
3. Enlargement of the same with nearly departing leaf trace 5, xylem cylinder (XC) with secretory cells (Sr), peripheral zone of the pith (P1), deformed outer part (D) of central region of the pith (P2), phloem (Ph) and innermost zone of the cortex (IMC). The arrow indicates the opening left on one side of the leaf trace where phloem is in contact with internal parenchyma (Pa). Slide WP2L-0029, scale bar = 200 µm.

Plate II. Stem of *Tiania yunnanense* gen. et comb. nov.

1. Detail of the stelar tissues: xylem cylinder (XC) showing one protoxylem strand (Px). Arrows indicate small and isodiametric cells at the outer margin of peripheral zone of the pith (P1). In contrast, the central region of pith (P2) consists of much broader cells which are deformed (D) at the periphery . Slide WP2L-0029, scale bar = 200 µm.
2. Longitudinal section through central region of the pith (P2 zone) showing longitudinally elongated thinner-walled parenchymatous cells. Slide WP2-0029, scale bar = 100 µm.
3. Longitudinal section showing thicker-walled cells from the periphery of the pith (P1 zone). Slide WP2-0029, scale bar = 100 µm.

4. Cross section through xylem cylinder, detail showing cells of the phloem (Ph), protoxylem strand (Px), parenchyma (Pa), secretory cells (Sr) and sclerenchyma (Sc). Arrows show cells with dark brown contents in the phloem. Slide WP2L-0030, scale bar = 100 µm.

5. Cross section through outer part of the stele showing tracheids of xylem cylinder (XC), well developed phloem (Ph), and innermost cortex (IMC); arrow showing a cell with dark brown contents in the phloem. Slide WP2L-0029, scale bar = 50 µm.

6. Longitudinal section of the xylem cylinder showing wide tracheids and longitudinally elongated parenchymatous cells (Pa). Slide WP2-0029, scale bar = 50 µm.

7. Longitudinal section through the outer part of the stele showing phloem cells (Ph) adjacent to metaxylem tracheids (XC) and innermost cortex (IMC). Slide WP2-0029, Scale bar =50 µm.

8. Longitudinal section of the stem showing periphery (P1) and central part (P2) of the pith, xylem cylinder (XC), a leaf trace (arrows) diverging from the stele at a narrow angle from the vertical and cortex (C). Slide WP2-0029, scale bar = 2 mm.

Plate III. Stem of *Tiania yunnanense* gen. et comb. nov. 1. Detail of stelar tissues showing an early stage of leaf trace initiation with one protoxylem strand (arrow) associated with parenchymatous cells (Pa) in xylem cylinder (XC). Slide

WP2L-0029, scale bar = 100 μm.

2. Higher level than that of Fig.1 in leaf trace initiation, with formation of the protuberance of the leaf trace xylem strand (LX), arrows indicating position of the two protoxylem strands of the future leaf trace; group of secretory cells (Sr) in xylem cylinder (XC). Slide WP2L-0029, scale bar = 200 μm.

3. Higher level than that of Fig. 2 showing a just diverging leaf trace from the xylem cylinder (XC) of the stem with an elliptical outline (arrow) and C-shaped xylem strand (LX). Slide WP2L-0029, scale bar = 200 μm.

4. Cross section through median region of the cortex, showing a leaf trace with distinct vascular bundle sheath (BS), phloem (Ph), xylem strand (LX) with protoxylem strands (short arrows), adaxial island of thick-walled cells (Is) and large secretory cells (long arrows). Slide WP2L-0029, scale bar = 200 μm.

5. Longitudinal section showing part of the cortex with large, longitudinally elongated secretory cells (arrows) and thick-walled cells (Is) in the adaxial concavity of leaf trace. Slide WP2-0029, scale bar = 100 μm.

6. Detail of a secretory cell in cortex with the content of tiny “particles” (arrows). Slide WP2L-0029, scale bar = 50 μm.

7. Longitudinal section of the xylem cylinder showing scalariform pitting on tracheid walls and secretory cells (Sr), arrows showing oblique tracheid end wall. Slide WP2-0029, scale bar = 100 μm.

Plate IV. Stem of *Tiania yunnanense* gen. et comb. nov. 1. Cross section of the stem showing the xylem cylinder (XC) at the bottom and inner region of the

cortex with several leaf traces and a sinuous root trace (RT). One just diverging leaf trace (arrowed) is somewhat elliptical in outline, while others are shallow C-shaped, each with an island of thick-walled cells (Is) in its adaxial concavity. Slide WP2L-0029, scale bar = 1 mm.

2. Cross section through outer part of the cortex showing several leaf traces with prominent bundle sheath (BS) and adaxial island of thick-walled cells (Is). Arrows indicate large secretory cells. Slide WP2L-0032, scale bar = 1 mm.
3. Cross section through periphery of the cortex showing a petiole base (PB) with a V-shaped xylem strand (LX) and several poorly preserved free roots (arrows). Slide WP2L-0032, scale bar = 1 mm.
4. Cross section through a leaf trace in the innermost part of the cortex with laterally departing root trace (RT), parenchyma (Pa) and well developed phloem (Ph). Arrows indicate position of three protoxylem strands. Slide WP2L-0029, scale bar = 200 µm.
5. Cross section of an individual root in the cortex showing its diarch xylem strand (St), inner cortex (IC) and outer cortex (OC). Slide WP2-0029, scale bar = 50 µm.

1. **Plate V.** Stem of *Tianiayunnanense* gen. et comb. nov. Cross section showing parenchyma cells of the cortex with obscure outline and tyloses-like contents; one cell with four tyloses-like contents (numbered 1-4) is outlined with a broken line and arrowed. Slide WP2L-0029, scale bar = 50 µm.
2. Cross section showing detail of thick-walled cells with conspicuous outline and tyloses-like contents in the adaxial concavity of the leaf trace. Slide WP2L-0029,

scale bar = 50 μm.

3. Longitudinal section through part of the cortex showing longitudinally elongated parenchyma cells with obscure outline and fully-filled tyloses-like contents (arrow); one cell with four tyloses-like contents (numbered 1-4) is outlined with a broken line and arrowed. Slide WP2-0029, scale bar = 100 μm.

4. "Secondary parenchyma" (SP) developed at the position of a leaf trace. Slide WP2L-0032, scale bar = 0.5 mm.

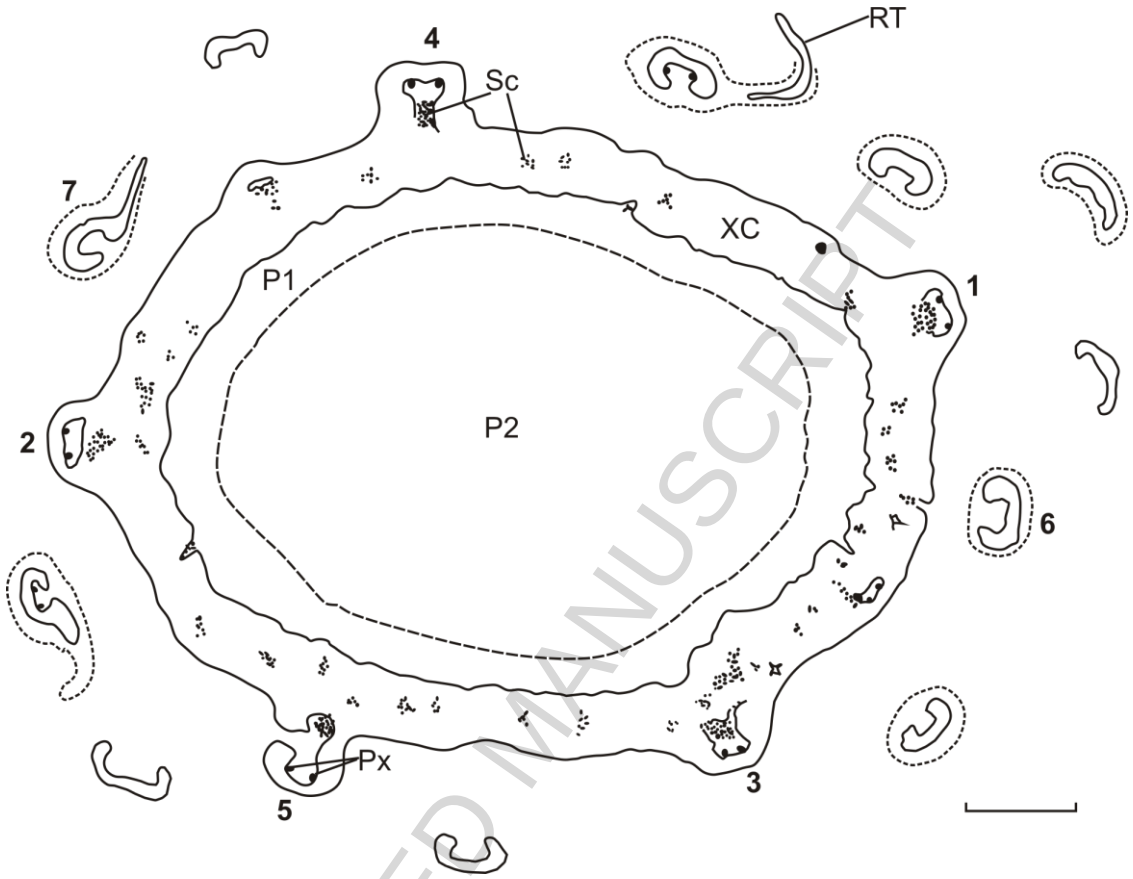

Fig 1

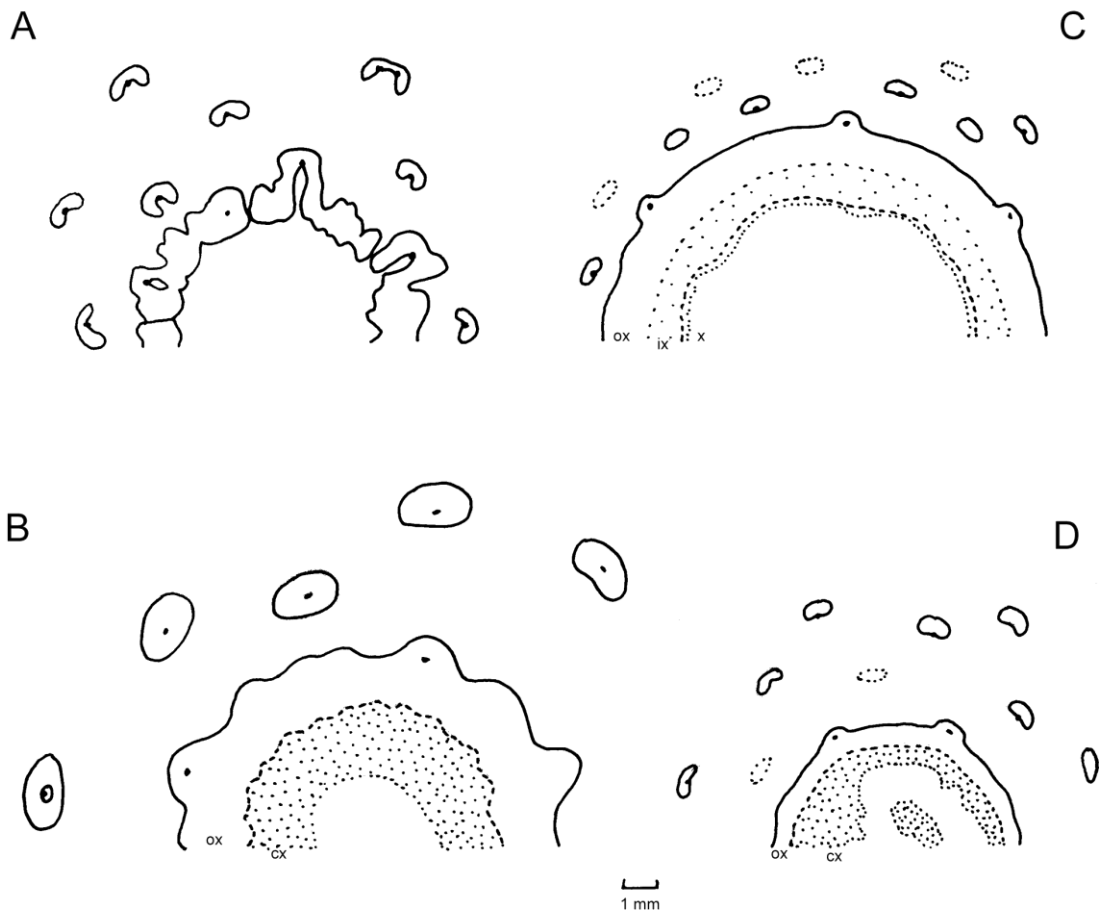

Fig 2

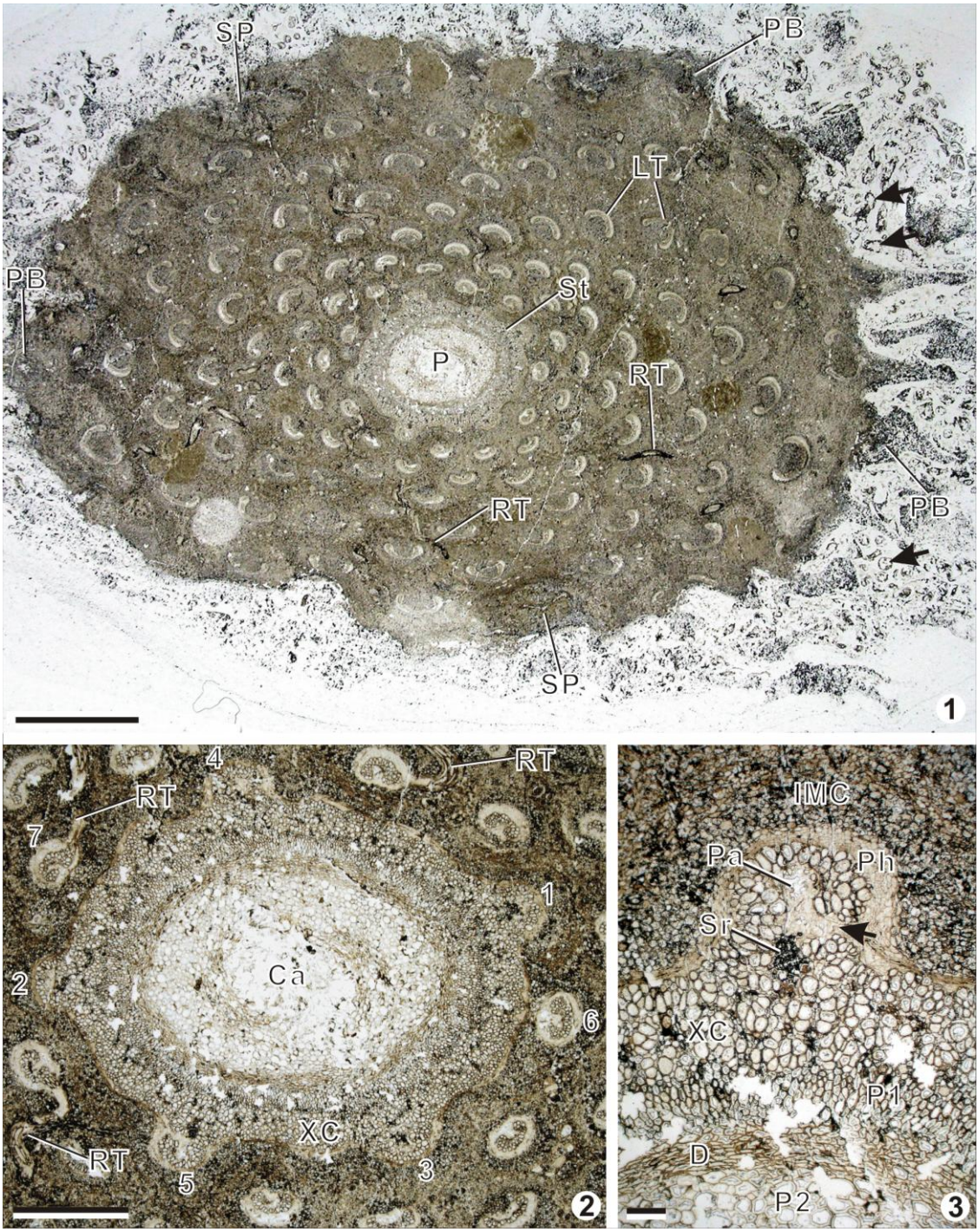

Plate I

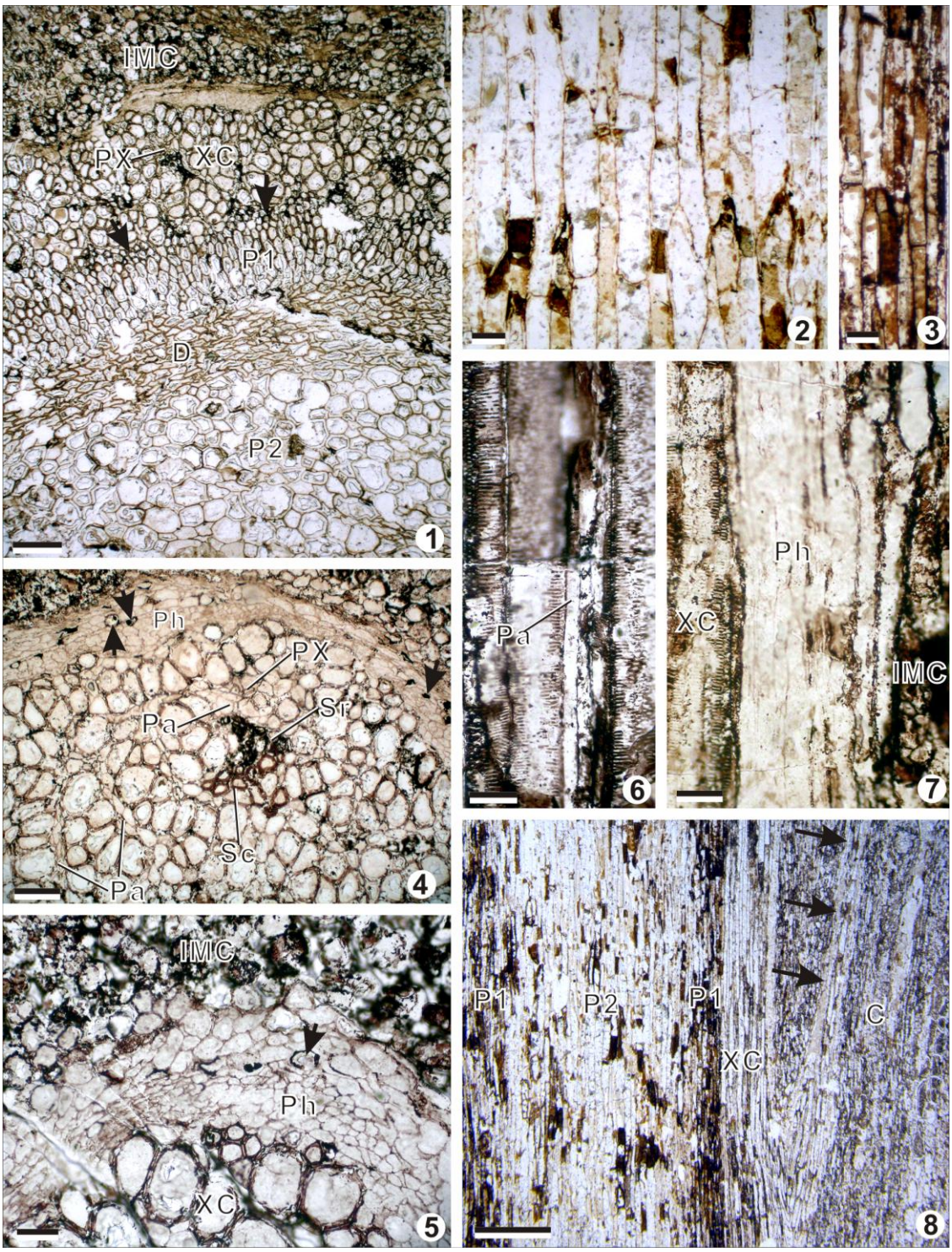

Plate II

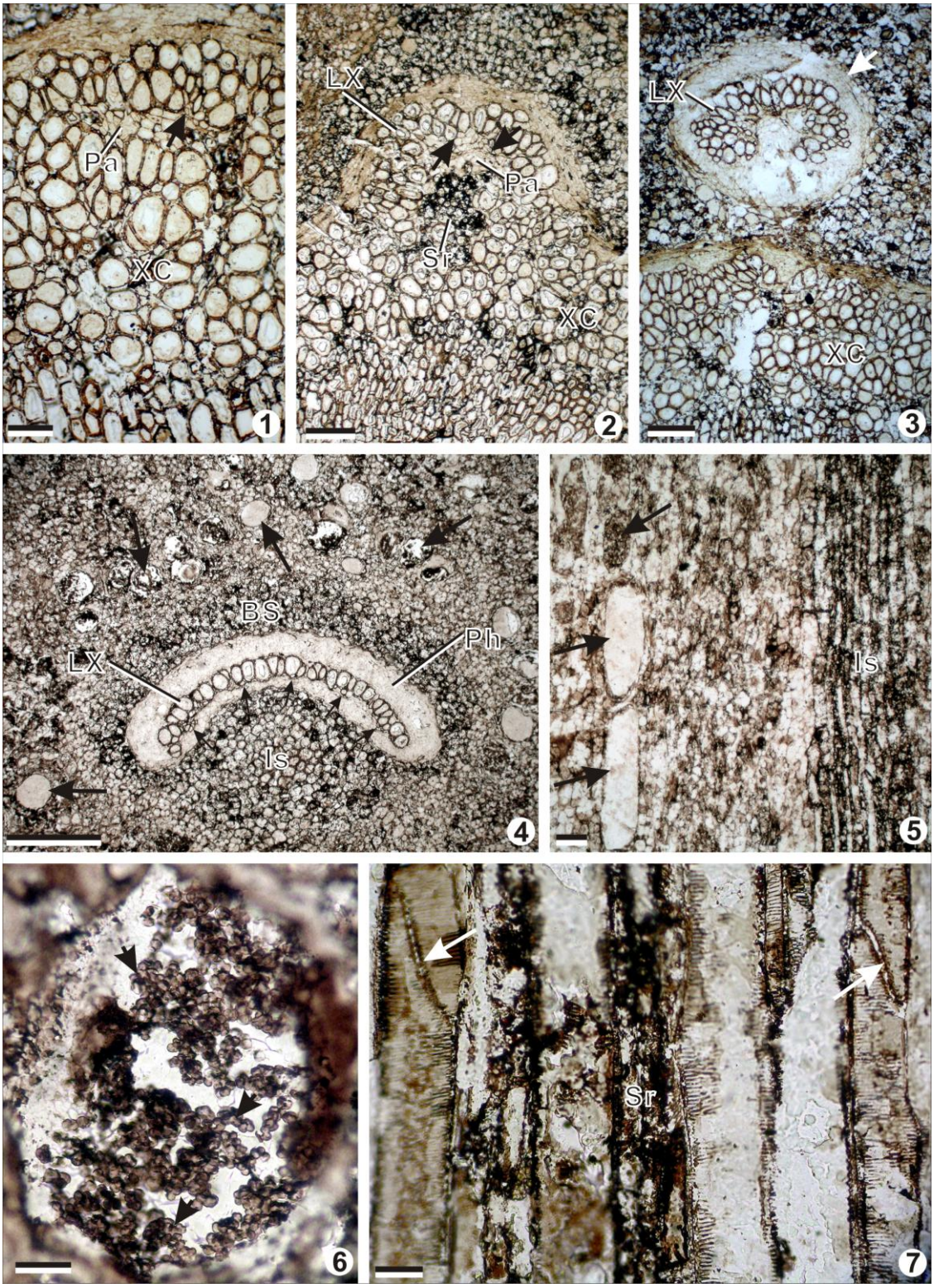

Plate III

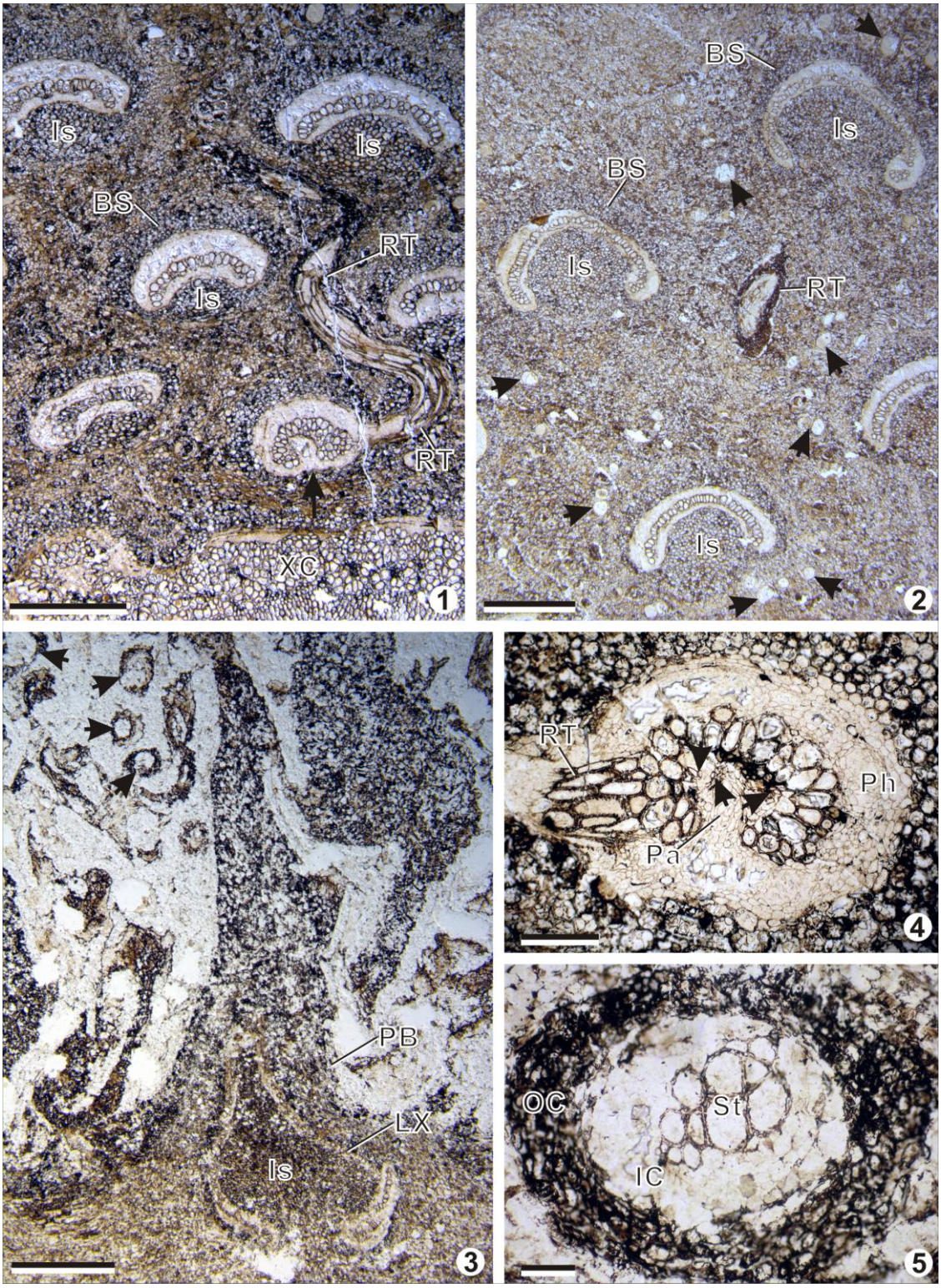

Plate IV

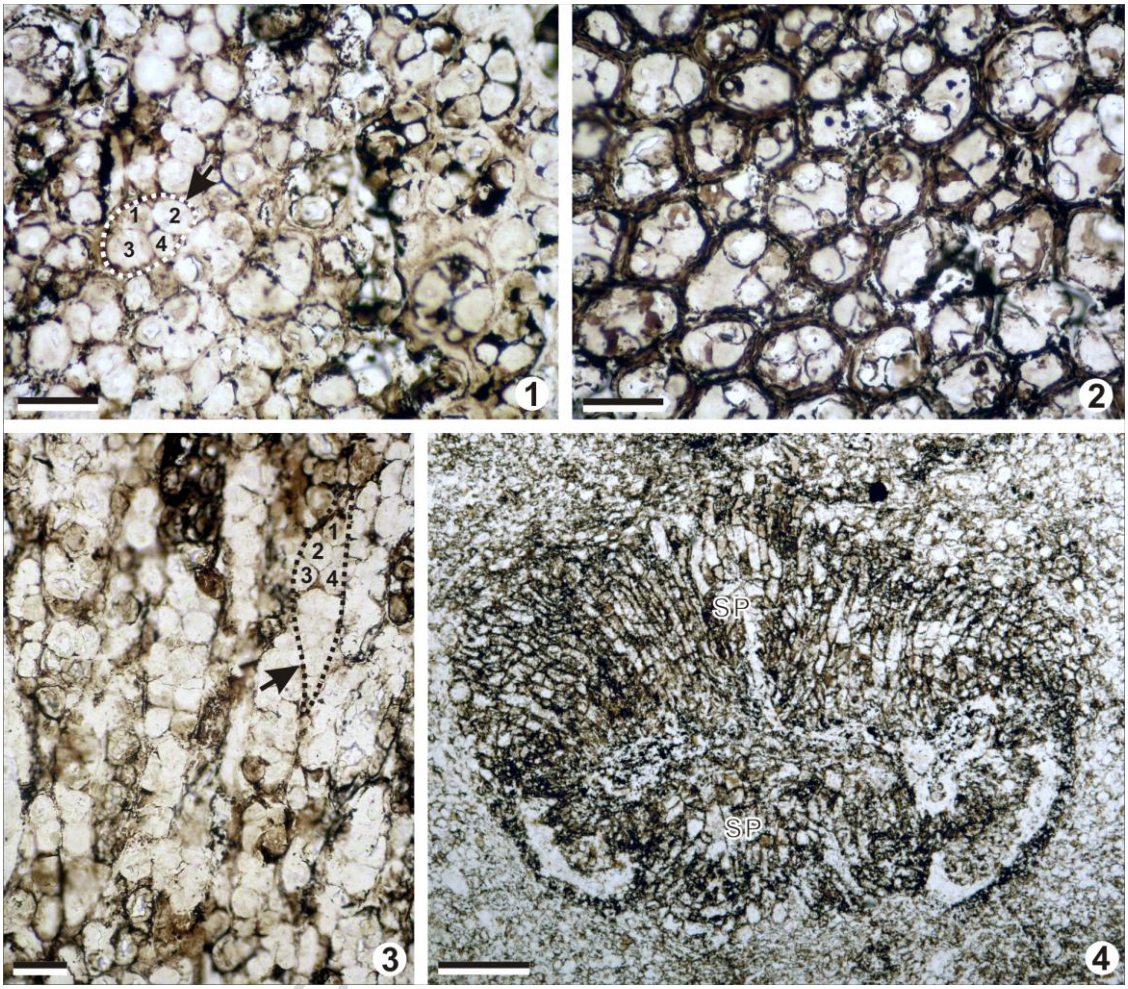

Plate V

ABSTRACT

The Permian aged osmundalean fern *Palaeosmunda yunnanense* Tian et Chang has been re-investigated based on the original specimens and demonstrated to represent a new genus within the extinct family Guaireaceae that we name *Tiania yunnanense* (Tian et Chang) gen. et. comb. nov. The stem of *T. yunnanense* is small, c. 30 mm in diameter, and comprises an ectophloic siphonostele without leaf gaps. Pith is bi-layered and consists of longitudinally elongated cells. Cortex is not differentiated into an inner parenchymatous and outer sclerenchymatous zone characteristic of members of the Osmundaceae, and possesses longitudinally elongated cells and large secretory cells. Leaf traces are numerous (>100) and adaxially curved, with two endarch protoxylem strands upon departing the stele, increasing to more than four protoxylem strands as the trace passes the cortex, all distributed along the adaxial side of the leaf trace. Leaf traces have more-or-less incurved lateral tips, and are encircled by a vascular bundle sheath. A mass of thick-walled, longitudinally elongated cells occur in the adaxial concavity of the leaf trace. Adventitious roots arise singly from the abaxial and lateral margin of individual departing leaf traces, and extend in a sinuous manner horizontally and longitudinally. Abundant tyloses-like contents occur in cells of the cortex and represent the first account of these within fossil Osmundales, but unlike other plant groups in which they occur within xylem, fibre-tracheids and lactifers, in *T. yunnanense* they occur in longitudinally elongated cortex cells where they presumably impeded fungal hyphae growth. Radially aligned 'secondary' parenchyma within the stem appears to represent a wound reaction in the cortex in the living plant. Due to its siphonostele

without leaf gaps, *Tiania* is interpreted as an evolutionary intermediate between the protostelic thamnopterids and the more advanced dictyostelic osmundaleans. Biogeographic implications of *Tiania* are discussed from which it is concluded that the Osmundalean diversity from the Late Permian of South China is unusually high and that these plants are likely to play an increasingly important role in our understanding of the early evolutionary history and systematic relationships of the Osmundales.

- *Palaeosmunda yunnanense* re-named *Tiania yunnanense* gen. et. comb. nov.
- *Tiania* placed within extinct Osmundalean family Guaireaceae
- Tyloses in longitudinally elongated cortex cells rather than in xylem
- Radially aligned 'secondary' parenchyma represents wound reaction tissue